THE SEPARATION OF POST–BASICORONAL AREAS FROM THE BASICORONAL PLATES IN THE INTERAMBULACRA OF THE SAND DOLLAR, ECHINARACHNIUS PARMA (LAMARCK)[1]

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One possible arrangement of the coronal plates of the central portion of the oral surface of the test of the sand dollar *Echinarachnius parma* (Lamarck) is shown as Figure 1. In this specimen the post-basicoronal interambulacral areas one through four are in contact with the basicoronal plates, but in interambulacrum five the post-basicoronal area has become separated from its basicoronal plate. Durham (1955) has indicated that the geologically younger genera of scutellinid echinoids tend to have the interambulacral columns separated from the basicoronal plates, whereas in the older genera these columns and plates are in contact. He also noted that in the Pacific Coast sand dollar, *Dendraster excentricus* (Eschscholtz), a member of one of the younger or more advanced genera, very small or young individuals had their basicoronal interambulacral plates in full contact with the succeeding plates and that as growth proceeds, the second plate of each ambulacral column grows faster than the others and eventually separates the second interambulacral plate from contact with the basicoronal interambulacral plate. Of all the species he studied for variation, *Echinarachnius parma* was found to be the most variable in respect to the separation of the interambulacral columns from the basicoronal plates. This study has been made with the aim of determining whether any pattern can be noted in this variation. With this in mind three questions are posed:

1. How many areas lose contact, and to what extent does this vary among specimens within and between collections from different localities?
2. Is there indication that there is any usual sequence among the areas in their loss of contact, and does this vary within and between collections from different localities?
3. Within areas retaining contact, are there differences in the amount of contact between first post-basicoronal plates "a" and "b" with the basicoronal plates? Is there any regular pattern of distribution of this asymmetry among the areas, and does this vary within and between collections from different localities?

Materials and Methods

Four series of specimens were collected intertidally, one series from each of the following places: Crow Neck, North Trescott, Washington County, Maine (44° 52′ 37″ N., 67° 07′ 38″ W.); Bailey's Mistake, South Lubec, Washington

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County, Maine (44° 46′ 23″ N., 67° 03′ 16″ W.); Hampton Beach, Rockingham County, New Hampshire (42° 54′ 07″ N., 70° 48′ 40″ W.); and Hampton Harbor, Rockingham County, New Hampshire (42° 53′ 59″ N., 70° 49′ 07″ W.). To minimize the possibility of the introduction of variability resulting from possible seasonal differences these collections were all made within as short a time period as feasible (September 12–15, 1962). Pertinent environmental characteristics of these collecting localities have been discussed by Lohavanijaya (1965).

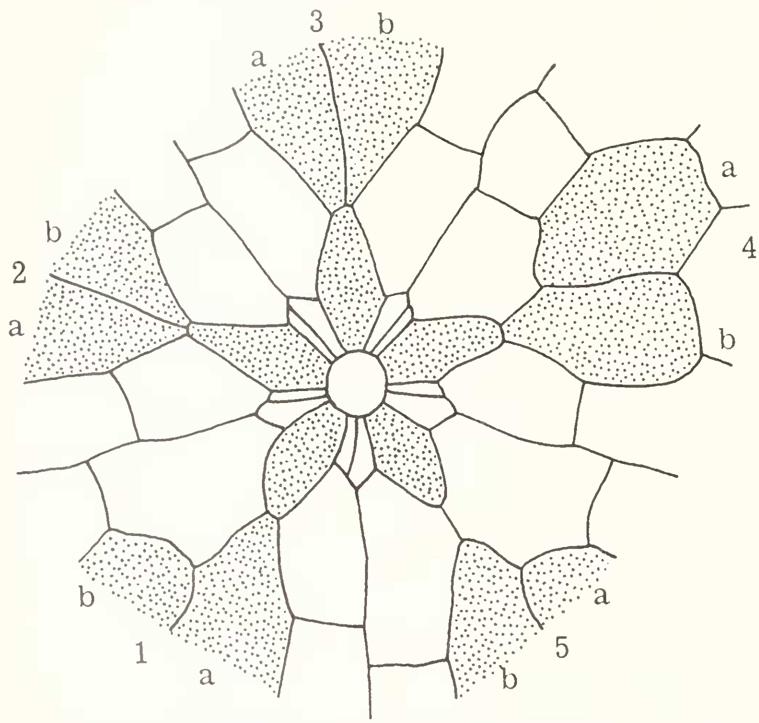

FIGURE 1. Oral surface of central portion of test of *Echinarachnius parma,* showing contact or lack of contact between basicoronal interambulacral plates and first post-basicoronal plates. Stippled areas are interambulacral and white areas are ambulacral.

More careful examination of the specimen shown in Figure 1 reveals not only that the post-basicoronal interambulacral areas 1, 2, 3, and 4 are in contact with their basicoronal plates, but also that the nature of this contact varies. In area 1 the first post-basicoronal plate "a" is in contact but "b" has lost contact, whereas in area 4 the situation is reversed. In areas 2 and 3 both "a" and "b" remain in contact, but it looks as though "b" were approaching loss of contact in area 3 while in area 2 the degree of contact appears more nearly equal.

In order to tabulate such variants for the large numbers of specimens studied, the following system of symbols has been devised.

If both plates "a" and "b" of the first post-basicoronal interambulacrals are "in contact" with the basicoronal to an approximately equal degree, the condition is designated: + +

If both plates "a" and "b" are "in contact" but "a" is to a greater degree, the condition is designated: + −

If both plates "a" and "b" are "in contact" but "b" is to a greater degree, the condition is designated: − +
If only plate "a" is "in contact," the condition is designated: + O
If only plate "b" is "in contact," the condition is designated: O +
If both plates "a" and "b" are "out of contact," the condition is designated: O O

Such data were compiled for the five interambulacral areas for a total of 1280 specimens. There were a few specimens for which these relationships could not

TABLE I

The nature of contact between first post-basicoronal interambulacral plates and basicoronal plates for the five areas of the oral surface of the test for series of specimens from four localities. N = the total numbers of specimens in each series. The numbers in the bulk of the table represent the numbers of specimens having each possible type of contact or absence of it (00) for each interambulacral area

Area	a b + +	a b + −	a b + 0	a b 0 0	a b 0 +	a b − +	N
BM* 1	2	56	72	161	1	1	293
2	32	19	5	85	36	116	
3	52	94	26	89	11	21	
4	2	0	0	116	98	77	
5	7	2	2	210	14	58	
CN* 1	8	73	106	105	2	1	295
2	30	17	5	68	79	96	
3	61	71	39	53	19	52	
4	2	3	1	88	109	92	
5	8	0	0	225	28	34	
HH* 1	11	149	76	68	0	7	311
2	50	67	7	60	22	105	
3	72	115	21	46	2	55	
4	7	3	0	65	70	166	
5	34	10	2	89	41	135	
HB* 1	39	171	68	44	37	11	370
2	122	58	6	31	19	134	
3	151	89	10	11	15	94	
4	39	18	1	58	56	198	
5	88	9	0	62	57	154	

* BM—Bailey's Mistake; CN—Crow Neck; HH—Hampton Harbor; HB—Hampton Beach.

be determined, a few that were malformed, injured, or otherwise so abnormal that they were not considered typical, and a very few so far from the usual sizes within each series that they were considered unusual. The specimens (23) in these categories have not been included in this study. The spines and the superficial organic material on the oral surface of the test were brushed off thoroughly. Then, in order to make the sutures separating the plates more readily visible, water was applied to the test. For determination of the nature of the contact between the basicoronal plates and the post-basicoronal areas, examination of the specimens

TABLE II

Comparison of frequency of occurrence of specimens with the "normal," "1st order" and "2nd order" deviant arrangements of interambulacral areas "out of contact" for specimens with 0, 1, 2, 3, 4 or all areas "out of contact" for Echinarachnius parma from the four localities studied

Series	# of specimens	% of collection	# of areas "out of contact"	Normal sequence		Deviant sequences			
						1st order**		2nd order**	
				#	%*	#	%	#	%
CN (15–70 mm.)	74	24.7	0	74	100.0	Not possible		Not possible	
	93	31.1	1	91	97.8	2	2.2	Not possible	
	36	12.0	2	18	50.0	18	50.0	0	0.0
	41	13.7	3	20	48.8	15	36.6	6	14.6
	34	11.4	4	13	38.2	15	44.1	6	17.6
	21	7.0	all	21	100.0	Not possible		Not possible	
Average number of areas "out of contact" per specimen = 529/299 = 1.77									
BM (50–90 mm.)	68	22.4	0	68	100.0	Not possible		Not possible	
	48	15.8	1	39	81.3	9	18.8	Not possible	
	45	14.9	2	29	64.4	14	31.1	2	4.4
	58	19.1	3	29	50.0	19	32.8	10	17.2
	40	13.2	4	18	45.0	15	37.5	7	17.5
	44	14.5	all	44	100.0	Not possible		Not possible	
Average number of areas "out of contact" per specimen = 692/303 = 2.28									
HB (20–59 mm.)	241	65.1	0	241	100.0	Not possible		Not possible	
	56	15.1	1	33	58.9	23	41.1	Not possible	
	21	5.7	2	9	42.9	4	19.0	8	38.1
	26	7.0	3	19	73.1	4	15.4	3	11.5
	14	3.8	4	11	78.6	3	21.4	0	0.0
	12	3.2	all	12	100.0	Not possible		Not possible	
Average number of areas "out of contact" per specimen = 292/370 = 0.79									
HH (40–65 mm.)	182	58.7	0	182	100.0	Not possible		Not possible	
	44	14.2	1	24	54.5	20	45.5	Not possible	
	26	8.4	2	2	7.7	12	46.2	12	46.2
	18	5.8	3	8	44.4	2	11.1	8	44.4
	22	7.1	4	11	50.0	4	18.2	7	31.8
	18	5.8	all	18	100.0	Not possible		Not possible	
Average number of areas "out of contact" per specimen = 328/310 = 1.06									

* These percentages refer to the percentage of specimens with the indicated number of areas "out of contact" having the sequence indicated.

** First order deviants are those presumed to be normal except for last one out of contact. Second order deviants are those combinations in which there appears to be aberrance in sequence in loss of contact prior to the last area involved.

with a hand lens was necessary. Each series of specimens was divided into size groups at 5-mm. intervals (except where numbers were inadequate). The data thus obtained were tabulated. In Table I these data are summarized by locality and area of test but without breakdown into size groups.

TABLE III

Distribution of numbers of interambulacral areas "out of contact" among different size groups of Echinarachnius parma from four localities

Series	Mean diameter ½ (L + W)	No. of specimens	Number of areas "out of contact"						Mean
			0	1	2	3	4	5	
CN	15–23.9	10	8	1	1	—	—	—	0.30
	27–34.9	7	4	1	1	1	—	—	0.86
	35–39.9	15	5	4	2	3	—	1	1.47
	40–44.9	38	11	12	2	5	6	2	1.71
	45–49.9	42	8	10	6	10	5	3	2.07
	50–54.9	63	12	22	11	7	8	3	1.78
	55–59.9	67	11	24	10	7	10	5	1.94
	60–64.9	38	11	13	2	5	4	4	1.76
	65–69.9	19	4	7	1	3	1	3	1.95
BM	50–54.9	30	7	9	3	4	6	1	1.87
	55–59.9	66	17	9	14	7	11	8	2.15
	60–64.9	59	21	8	4	13	5	8	1.95
	65–69.9	52	5	11	7	11	7	11	2.71
	70–74.9	46	6	4	11	11	4	10	2.72
	75–79.9	40	12	5	5	10	3	5	2.05
	80–84.9	10	—	2	1	2	4	1	3.10
HB	20–24.9	19	18	1	—	—	—	—	0.05
	25–29.9	24	22	2	—	—	—	—	0.09
	30–34.9	51	39	6	3	1	—	2	0.49
	35–39.9	56	37	11	3	2	1	2	0.66
	40–44.9	91	59	12	4	9	5	2	0.85
	45–49.9	81	46	16	5	8	3	3	0.95
	50–54.9	38	16	7	4	6	2	3	1.47
	55–59.9	10	4	1	2	—	3	—	1.70
HH	40–44.9	15	9	2	—	1	2	1	1.20
	45–49.9	75	44	12	7	4	5	3	0.97
	50–54.9	121	71	19	8	7	7	9	1.07
	55–59.9	83	54	7	9	4	4	5	0.94
	60–64.9	16	4	4	2	2	4	—	1.88

NUMBERS OF AREAS OUT OF CONTACT

In Table II several kinds of data are tabulated. The first column on the left indicates the number of specimens from the locality indicated having 0, 1, 2, 3, 4, or all areas "out of contact." In the next column these numbers have been converted into percentages of the total number of specimens used in this study from each locality. Then under the tabulations for each locality the average number of areas "out of contact" per specimen for the collection from the locality has been calculated. The average numbers of 1.77 for Crow Neck, 2.28 for Bailey's Mistake, 0.79 for Hampton Beach, and 1.06 for Hampton Harbor suggest that the Maine localities have populations that are more progressive in this respect than are those from the New Hampshire sites. Noting the size ranges from the localities (indicated on the table under the initials for the name of each locality) and recalling that numbers of areas "out of contact" presumably increase as the animals grow, one is immediately beset with the question: Are these differences the result of differences in environmental induction or selection on the one hand, or are they wholly the result of the differences in size-composition among the collections? Table III and

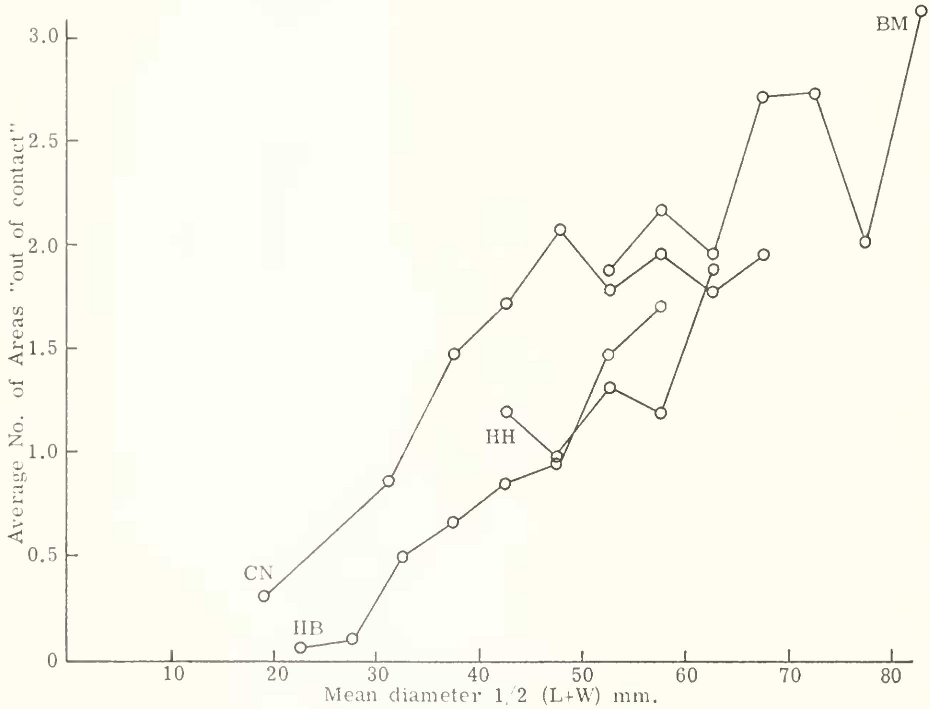

FIGURE 2. Relationship of the average number of areas "out of contact" to size ½ (L+W).

Figure 2 have been assembled to show the mean numbers of areas "out of contact" at 5-mm. size (mean diameter) intervals for each of the localities. It is obvious that much larger collections and smaller size intervals would be needed to give smooth curves on the graphs, but it is quite apparent that:

(1) For comparable mean diameters up to at least 55 mm. the mean number of areas "out of contact" is higher for the Crow Neck collection than for either Hampton Beach or Hampton Harbor, and

(2) In the range of diameters between 55 and 70 mm. there appears possibly to be a tendency toward equal numbers of areas "out of contact" for all the localities. Thus for mean diameters of 62.5 mm., the mean numbers of areas "out of contact" for the collections from Crow Neck, Bailey's Mistake, and Hampton Harbor all

fall within the range between 1.75 and 2.00. Although none of the specimens from Hampton Beach is this large, extrapolation of the plotted values for smaller sizes into this range would place the expected value for this locality very close to 2.00 areas "out of contact."

Apparent Sequence of Loss of Contact in Interambulacral Areas

All possible combinations of areas "out of contact" were listed, and for each locality the number of specimens having each combination was tallied. Examination of these data along with Durham's (1955) Table 3 (p. 108) strongly suggested that the usual sequence in which interambulacral areas lose contact is 5, 1, 4, 2, 3. Thus, one would expect specimens "out of contact" for a single area to be most frequently "out of contact" in area 5. When two areas are "out of contact," areas 5 and 1 should be the most frequent combination. This would continue, and the whole expected sequence would thus be 0→5→5 & 1→5, 1, & 4→5, 1, 4, & 2→5, 1, 4, 2, & 3

Table IV

All possible combinations of normal, 1st order deviants, and 2nd order deviants

Areas "out of contact"	Normal	1st order deviants	2nd order deviants
0	All	Not possible	Not possible
1	5	1; 2; 3; or 4	Not possible
2	5 & 1	5, 2; 5,3; or 5,4	1, 2; 1, 3; 1, 4; 2, 3; 2, 4; or 3, 4
3	5, 1 & 4	5, 1, 2; or 5, 1, 3	1, 2, 3; 1, 2, 4; 1, 3, 4; 2, 3, 4; 2, 3, 5; 2, 4, 5; or 3, 4, 5
4	5, 1, 4 & 2	5, 1, 4 & 3	1, 2, 3, 4; 1, 2, 3, 5; or 2, 3, 4, 5
5 (all)	All	Not possible	Not possible

(= all areas). These combinations are hereafter called members of the normal sequence. Durham's (1955) data for his series from Woods Hole, Massachusetts, and the data here presented in Table II for Crow Neck, Bailey's Mistake, and Hampton Beach support this sequence, or at least the resulting combinations that may be obtained through it. Thus, these combinations of areas "out of contact" are the most frequently occurring combinations in the collections aforementioned. Durham (1955) noted that the small collection (21 specimens) he studied from Hampton Harbor exhibited great variation in respect to loss of contact among the interambulacral areas. In the present study 310 specimens were examined from this locale, and Durham's conclusion is abundantly supported as can readily be seen from examination of Table II.

The variants from these usual combinations may be conveniently divided into two categories. Cases where combinations include areas "out of contact" in the normal combination, except for the area presumed last to lose contact, are termed "first order deviants." Thus, any specimen having one area "out of contact" other than area 5 would be a "first order deviant." "First order deviants" with two areas "out of contact" must have one of these areas 5, and the other must not be area 1. "Second order deviants" are those combinations which do not include the presumed penultimate area among those "out of contact." Thus, for specimens with two areas "out of contact," a "second order deviant" must not include area 5 among the areas "out of contact." In Table IV all possible combinations of "normal," "first order deviants," and "second order deviants" are indicated. All the theoretically possible combinations have actually been observed among the 1282 specimens dealt with in this section, except 2, 3 and 4.

Tables V and VI indicate the numbers of each particular deviant found in each collection. In Table II the occurrence of "normal," "first order deviant," and "second order deviant" combinations are totalled for each collection for each number of areas "out of contact."

Table V

Number of specimens of 1st order deviants in each collection

Areas "out of contact"	1st order deviants	CN	BM	HB	HH	Total
0	Not possible					
1	1	0	3	15	7	
	2	0	3	1	6	
	3	1	3	1	5	
	4	1	0	6	2	
		—	—	—	—	
		2	9	23	20	54
2	5 & 2	11	6	0	4	
	5 & 3	2	2	1	2	
	5 & 4	5	6	3	6	
		—	—	—	—	
		18	14	4	12	48
3	5, 1 & 2	7	6	3	2	
	5, 1 & 3	8	13	1	0	
		—	—	—	—	
		15	19	4	2	40
4	5, 1, 4 & 3	15	15	3	4	37
5 (all)	Not possible					—
						179

Examination of these tables reveals that for the collections from Crow Neck and Bailey's Mistake, Maine, and Hampton Beach, New Hampshire, it is almost a generalization that for each number of areas "out of contact" there are more specimens with "normal" arrangements than with either first or second order deviant arrangements. The unique exception to this statement occurs among the specimens from Crow Neck with four areas "out of contact." Among these 38.2% have the "normal" arrangement and 44.1% have the only possible first order deviant arrangement—that is, areas 5, 1, 4, and 3 "out of contact." There are, however, a few other situations (numbers of areas "out of contact" for given localities) where the sum of the first and second order deviants exceeds the number of "normal" individuals. But for the exception noted above, however, in no case does the number of individuals with any specific deviant even approach the number of "normal" individuals in these localities.

For the collection from Hampton Harbor the situation is quite different. Although there is still a majority of these specimens with one area "out of contact" having the normal area 5 "out of contact," the percentage of these is much lower than found for the Maine localities and somewhat less than at Hampton Beach. In the group with two areas "out of contact" there is a total of only 26 specimens.

TABLE VI

Number of specimens of 2nd order deviants in each collection

Areas "out of contact"	2nd order deviants	CN	BM	HB	HH	Total
0	Not possible					
1	Not possible					
2	1 & 2	0	0	1	1	
	1 & 3	0	0	0	2	
	1 & 4	0	2	5	3	
	2 & 3	0	0	1	2	
	2 & 4	0	0	1	3	
	3 & 4	0	0	0	1	
		—	—	—	—	
		0	2	8	12	22
3	1, 2 & 3	0	1	0	1	
	1, 2 & 4	0	2	1	1	
	1, 3 & 4	0	1	0	1	
	2, 3 & 4	0	0	0	0	
	2, 3 & 5	3	4	0	3	
	2, 4 & 5	2	0	2	2	
	3, 4 & 5	1	2	0	0	
		—	—	—	—	
		6	10	3	8	27
4	1, 2, 3 & 4	1	0	0	4	
	1, 2, 3 & 5	1	5	0	2	
	2, 3, 4 & 5	4	2	0	1	
		—	—	—	—	
		6	7	0	7	20
5 (all)	Not possible					—
						69

Of these only two (7.7%) have the "normal" arrangement. While not much significance can be attached to these small numbers, it is interesting to note that the first order deviant arrangements of areas 5 and 4, and 5 and 2 and the second order deviants 1 and 4, and 2 and 4 "out of contact" all exceed the "normal" arrangement. These conditions suggest a tendency for areas 4 and 2 to lose contact ahead of sequence. Durham's (1955) data for this locality also indicate the tendency for area 4 to precede area 1. Second order deviants for specimens with three or four areas "out of contact" are also exceptionally high in this collection.

Here again we suffer from small numbers, but the tendency could be readily explained on the basis of deviant sequences early in their development.

Why the sequence of loss of contact among the interambulacral areas is so unusual at Hampton Harbor is a difficult question to approach. It seems incomprehensible that the Hampton Harbor population is genetically isolated from those of Hampton Beach hardly a mile distant by interconnecting water. However, there still exists the possibility that even from a common gene pool and common reservoir of larvae, there could be a selective difference of survival among genotypes

Table VII

Numbers and percentages of specimens, asymmetrical around the interambulacral radii, having more contact with "a" than "b" (+ − and +0) and having more contact with "b" than "a" (0+ and − +) according to area of test and locality of collection

Area	Series	+ − and + 0		0 + and − +	
		No.	%	No.	%
1	CN	179	98.4	3	1.6
	BM	128	98.5	2	1.5
	HB	239	83.3	48	16.7
	HH	225	97.0	7	3.0
2	CN	22	11.2	175	88.8
	BM	24	13.6	152	86.4
	HB	64	29.5	153	70.5
	HH	74	36.8	127	63.2
3	CN	110	60.8	71	39.2
	BM	120	78.9	32	21.1
	HB	99	47.6	109	52.4
	HH	136	70.5	57	29.5
4	CN	4	2.0	201	98.0
	BM	0	0.0	175	100.0
	HB	19	7.0	254	93.0
	HH	3	1.3	236	98.7
5	CN	0	0.0	62	100.0
	BM	4	5.3	72	94.7
	HB	9	4.1	211	95.9
	HH	12	6.4	176	93.6

after metamorphosis. The other likely explanation is that the differences in environmental factors between these proximate localities may affect genetically-like organisms in such manner that they develop differently. Regardless of whether these differences are genetic or environmentally induced, there still remains the question as to what environmental factors might be involved. A somewhat similar problem concerning variation in the heart-urchin, *Echinocardium cordatum* Pennant, as it occurs in British and nearby waters has been carefully studied by Nichols (1962), who suggests functional advantages for the variants he studied and favors the explanation of differences between populations as resulting from differential selection.

Asymmetry within Interambulacral Areas

Differences in the amount of contact between first post-basicoronal plates "a" and "b" with the basicoronal plates cause deviations from the symmetrical arrangements of plates on the two sides of the radius running through the middle of the area in question.

Table I summarizes the number of individuals having the various types of contact, or lack of it, between the first post-basicoronal plates and the basicoronal plates for each of the interambulacra in the specimens collected from Bailey's Mistake and Crow Neck, Maine, and Hampton Beach and Hampton Harbor, New Hampshire. Inspection of this table indicates that in areas 1, 2, 3, 4, and 5, plates "b", "a", "b", "a", and "a", respectively, appear to lose contact more frequently ahead of the other member of the pair. It can readily be seen from Table VII that the degree of preponderance varies among the areas and within areas among the collections from different localities.

Discussion

The loss of contact between first post-basicoronal interambulacral plates and the basicoronal plates varies in respect to number of areas involved, apparent sequence among areas, and in the asymmetry of contact within the areas which appear to be in the process of losing contact. The number of areas "out of contact" is subject to increase as the individual grows—at least initially. Thus, specimens with (or populations averaging) more areas "out of contact" may be thought of as being more advanced or progressive. This agrees with Durham's (1955) idea that primitive genera and species near the ancestral stock retain contact whereas more highly evolved taxa are characterized by increasing loss of contact. Among the regular echinoids Jackson (1912) on similar grounds considered the exsert condition of ocular plates to be primitive and the insert condition more progressive. From the studies of Jackson (1912), Vasseur (1952), and Swan (1958, 1962) it appears that for *Strongylocentrotus* higher salinities and lower temperatures go hand in hand with the more progressive development characterized by more ocular plates insert. For the tropical *Tripneustes,* however, Jackson's (1914) data suggest the opposite relationship with temperature. *E. parma* is essentially a boreal species, and the higher numbers of areas "out of contact" in the collections from Maine, indicating that they are more progressive, might suggest that this species, like *Strongylocentrotus,* attains a more progressive condition in cooler water. Much caution should be used, however, in making even tentative conclusions on the basis of these few data. One cannot determine a trend from two points (the New Hampshire series as compared with those from Maine) ; and when the mean number of areas "out of contact" is calculated for Durham's (1955, Table 3, p. 108) series of *E. parma* from Woods Hole, Massachusetts, the value obtained is 1.71. At first glance it is apparent that this figure is nearly up to the overall average value for Crow Neck, Maine; but when the effect of the size of the specimens is considered, conclusions based on comparison of these overall averages become obviously questionable. If the specimens Durham (1955) used for his Table 3 are the same ones used for Table 2, which were said to range from 50 to 62 mm. in average diameter, they are in the size range where a convergence in numbers of areas "out of contact" occurs among the collections from Maine and New Hampshire and thus indicate little.

This convergence, as shown in Figure 2, makes one wonder if the loss of contact by additional areas may not cease when a certain size or age is reached. As shown by Jackson (1912) and verified by Swan (1958), this appears to be the case for ocular plates becoming insert in *Strongylocentrotus droebachiensis.* The arrangement of points (Fig. 2) relating average numbers of areas "out of contact" to mean diameter for the sand dollars from Crow Neck certainly appears to suggest a curve becoming asymptotic to the base line at some value between 1.75 and 2.00 areas "out of contact" for diameters above about 45 mm. For diameters of 45 mm. and less the "curve" for the population from Hampton Beach appears to be roughly parallel to that for Crow Neck but is displaced toward lower numbers of areas "out of contact" at comparable diameters. There is no indication of flattening out of this curve at mean diameters near 45 mm., and no specimens were available for sizes that were appreciably above the diameters where the mean number of areas "out of contact" reached 1.70. The size ranges of the series from Bailey's Mistake and from Hampton Harbor are such that they give little help toward answering questions, but the great fluctuation shown in the series from Bailey's Mistake in regard to numbers of areas "out of contact" intensifies another question suggested by the "curve" representing the Crow Neck population. If there is a limit beyond which no further areas lose contact, does the value of this limit fluctuate? If so, why? These remain as problems for future attack. Before leaving this subject, we should be reminded of the fact that Durham's (1955) findings would suggest that in sand dollars new plates on the oral side of the test are added up to a certain small size, after which no more are added. The variation he notes in the numbers of these plates in *E. parma* might be related to differences in the time at which their addition ceases in different individuals. That the addition of coronal plates may cease before regular urchins die or cease growing is indicated by Hsia (1948) for two species of *Temnopleurus.* No work is known to the present authors which indicates whether or not the size or number of plates at which this occurs varies within the species from one population to another. Again the temptation to make comparisons with better known organisms in other phyla is strong. A great many studies have been made on the numbers of vertebrae, fin-rays, and other serially repeated structures in fishes; and generally it appears that longer developmental periods (*i.e.*, slower growth through the critical stages in development) produce higher counts in meristic structures. Low temperatures, high salinities and low oxygen tensions have been shown to retard development and produce this effect. Much of the pertinent literature on this subject has been discussed and listed by Barlow (1961). That light may also affect the number of vertebrae formed appears to be the case in at least some instances (McHugh, 1954). Perhaps it is no mere coincidence that *Strongylocentrotus* appears to progress further in its attainment of insert ocular plates in colder or more saline waters and that *Echinarachnius* tends to progress toward having more interambulacral areas "out of contact" in eastern Maine than in New Hampshire. It would be interesting to check the numbers of plates on the oral surfaces of the series from colder and warmer water to see if those from colder water had a higher average number.

The sequence of 5, 1, 4, 2, 3 in which interambulacral areas lose contact is of more than a little interest. Although in *Strongylocentrotus* the normal sequence in which oculars become insert is I, V, IV, II with no record of all oculars insert, there are many genera of regular urchins where the normal sequence is V, I, IV, II, III (Jackson, 1912). Jackson (1912, 1914), Vasseur (1952), and Swan (1962) have all noted that localities differ from one another in respect to the frequency with which aberrant variant combinations of oculars insert occur in various species of regular urchins. Thus, the fact that one of the localities here studied (Hampton Harbor) is characterized by so many deviant arrangements of areas "out of contact" among its sand dollars is not surprising, but at present no explanation can be suggested. Swan (1962) has noted that certain aberrant variant arrangements of ocular plates insert in *Strongylocentrotus* are indicative of *"situs inversus."* The possibility that some of the deviant arrangements of areas "out of contact" in *Echinarachnius* may also indicate such deep-seated reversals of asymmetry should be more carefully checked. Initial examination of the first post-basicoronal ambulacral plates revealed no deviations from conformity with Lovén's (1874) law (*cf.* p. 104, Durham, 1955) that would suggest a reversed pattern. If all specimens or any suspected of being reversed were cut frontally or examined with a fluoroscope, it should be possible to determine the course traversed by the digestive tract and get the best evidence from internal anatomy.

The pattern of asymmetry around the central axes through the interambulacral areas is very strongly marked in areas 1, 4, 5, fairly strongly marked in area 2, and rather weakly marked in area 3. It is possible that the deviations from the usual arrangements here too might be symptomatic of the more deep-seated *"situs inversus."* In some respects this study may be considered as an extension of Durham's (1955) notable work, which owed a great deal to the earlier thinking of numerous workers, of whom Lovén (1874) and Jackson (1912) must be singled out as especially important. At the same time it is obvious that in the present work there are more new avenues of investigation suggested than problems completely solved. Workers desirous of making additional studies of variation in irregular urchins should, in addition to the approaches used here, become thoroughly acquainted with the methods of Kongiel (1938), Kermack (1954), Nichols (1959a, 1959b, 1962) and Kier (1962).

Summary

1. The general arrangement of plates on the oral surface of sand dollars is discussed.

2. Variations in this arrangement as they occur in *Echinarachnius parma* from several New England localities are indicated.

3. As this sand dollar increases in size, there is decreasing contact between the post-basicoronal interambulacral areas and the basicoronal plates.

4. The usual sequence in which this contact is lost among the areas is 5, 1, 4, 2 and 3, but all possible combinations of areas "out of contact" have been observed, except 2, 3 and 4.

5. The average numbers of areas "out of contact" for animals of comparable sizes vary among localities.

6. The asymmetry of loss of contact within the interambulacral areas has also been found to be highly variable.

7. The possibility that these variations may be related to differential environmental effects upon the rates at which different parts of the growth process occur is suggested.

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